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Topological and mechanistic explanations in biology

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It has often been argued that to explain means to point out the causes of some event, phenomenon, state of affairs, etc. (e.g. Salmon, 1984), and then uncover mechanisms (Machamer et al. 2000). In this paper, I will focus on a kind of explanation that is not straightforwardly causal, and which becomes more and more pervasive across many disciplines, i.e. ecology, social sciences, molecular biology, evolutionary biology or cell biology.

I first specify the differences between what I will call "mechanistic" and "topological" explanation. Then I consider a major set of topological explanations in ecology. Finally I consider mechanisms and topologies as the varieties of explanation of robustness of various kinds of living systems.

Topological vs. mechanistic explanations

When we explain a phenomenon, we generally consider how the system from which it is a property, an outcome, a characteristic or a consequence behaves. We may try to determine causal relations, or to subsume several features of the system and its functioning under some laws of nature – those two concerns not being mutually exclusive. The system considered may have many properties. Some of them concern how, to put it vaguely, it fills a space; how parts of the system are located regarding one another, and whether those relations can still hold under some continuous deformations of the system (and which ones). Those are what I call the topological properties of the system. But the "parts" are not restricted to the physical parts of the system as a material entity; they can be parts of a more abstract space, possibly a mathematical hyperspace, and then be involved in such topological properties. For example, an ecological community is a set of individuals of various species: *prima facie* its parts are the

organisms; but on a more abstract level, one can see the species as parts. Those species have relations, for instance they prey on one another. The schema of their predation relationships is therefore a feature of the system; it takes place in a space, and can display topological properties.

I call a topological explanation, an explanation in which a feature, a trait, a property or an outcome X of a system S is explained by the fact that it possesses specific topological properties T_i. What "possess topological properties" means is the following: S has elements, parts, features or capacities, moments of its regular behavior, or of the set of its possible behaviors, which are likely to be represented in a graph, a network or a variety S' in a space E. (For instance, the phase space of the system can be such a space.)

You can define a topological space on E. Once this topology is defined, S' will have topological properties T_i, namely, properties which specify its invariance under some continuous transformations, and which will determine equivalence classes between all structures S'' homotopic to S'. Or, if S' is a graph, you can specify some properties of S' (e.g. connexity; cyclicity, etc.) which will define an equivalence class, and distinguish S' from other graphs S* not having those properties. Topology or graph theory thus provides tools to classify S' within specific categories defined by the properties they have. From now on, I call "topological properties", those properties that are either proper to subsets in a topological space or to some graphs and networks.

Topology and graph theory *stricto sensu* are not the same mathematic subfields. Those two fields, topology and graph theory, have indeed been joined in a topological graph theory, currently developed for its own sake (Gross and Tucker 1987). In the following, I consider both fields together because they are working in the same way with respect to what I am calling topological explanations, namely they specify the nature of the properties whose existence entail the fact that the explanandum happens. S has topological properties in virtue of its relation to S' and its elements and relations.

The topological explanatory relation implies that whatever possible process B_j occurs to S that involves some or all elements or parts of S, no B_j is necessary to account for X, but the simple fact that S realizes T_i entails as a consequence the fact that S has X. We therefore have a topological explanation when none of the B_j is needed to explain. It

may be that a given X causally results from some B_j, but that what explains X is not the B_j itself; the reason would be that another causal process B_k also produces X, but that the topological properties T_i which constrain in the same way all processes T_i, entail that whatever the process B_j, the outcome will be of type X, so that the causal process B_j itself does not make any difference (conditionally on the fact of T_i) to the outcome and is therefore not explanatory. And unlike a mechanism or a process, a topology is not something that takes place in time: so those kinds of explanations are of very different kind than the uncovering of mechanisms or the understanding of specific processes. Explanation of X goes like a relation of entailment between topological properties T_i and X or features of X, and not like the display of a mechanism from which X would be a temporal outcome.

I draw this contrast between B_j and T_i to emphasize the fact that topological explanations are exclusive of explanations which pinpoint some mechanisms, or some specific causal interactions between elements of S underlying mechanisms, as explanatory relevant. What are at stake when someone unravels a mechanism or a process are the specific causal relations uncovered between elements. However, in the explanations considered here, those specific causal relations are irrelevant; what counts is the fact that there are relations in S', the associated shape of S in space E, because the patterns of relation in S' can define a topological structure with its properties realized by S and then be explanatory of X.

The topological explanations of ecological stability

The relationship between the diversity of species in an ecological community and the stability of this community is a longstanding debated topic in ecology (McCann 1998). Although often supported by ecologists, the idea that diversity would yield stability was not demonstrated until the 1970s. May (1974) formally demonstrated that in fact, if you consider that species are randomly connected, more diversity would imply less stability in terms of the constancy of frequencies of individuals. This prompted ecologists to realize that the exact meanings of stability and diversity were central issues. Functional diversity, for example, cannot be equated with *number* of species, since one could

have many species preying on the same preys, being therefore functionally equivalent. And as it turned out, if stability is understood as the constancy of some property like the biomass (Tilman, 1996), then diversity enforces it. So many varieties of diversity-stability hypotheses, often involving complexity (Pimm, 1984), flourished during the past two decades. (Pimm, 2001). Some of those (Solé and Montoya 2001; Dunne et al. 2002; McCann et al. 1998; Montoya and Solé 2002; Montoya et al. 2006 – after Yodzis 1989; Dunne 2006) considered only three parameters describing diversity: the number of species and their average number of links, the number of connections realized between species as compared to the number of possible connections (connectance), and the distribution of the connections between species. These hypotheses provide examples of topological explanations.

The general aim of these studies consists in specifying for a community S the network S' of relationships between species, each interaction being represented by a link, and then inferring from properties of this network some properties concerning stability, resilience, etc. In ecology, two species can have several kinds of causal relations: A can prey on B, be the prey of B, compete with B, be mutualistic or commensal with B, or parasitic on B, for example. However, in those networks, the nature of interactions between species - whether A preys on B, or is parasitic on B, or is preyed on by B etc. - is not relevant, but only their number and the global shape of the connections between them as represented by a graph (Montoya et al. 2006).

If we want to explain why an ecological community is stable, or which communities are more likely to be stable, we can consider how they react to invading species, or extinction of some of their species. The stable ones are the communities where those events don't have many consequences upon the repartition of species or the frequencies of individuals in those species; the less stable are the ones that undergo dramatic changes in composition. There can be a simple ecological explanation for that: suppose that an ecological network has a few hubs that are vastly connected, and many species that are not very connected. Concretely, you can identify an omnivore species, therefore being a hub connected to many species, and then species specialized on only one prey, which will comprise isolated nodes. Now a random deletion of species will be more likely to touch a weakly connected node: suppose that each species is equiprobably likely to be

deleted, and that you have two hubs and 464 simple nodes; then of course the deletion has 232 more chances to delete only an isolated node. So the whole structure of links won't be altered, therefore the whole community will have some stability, in terms of response to species extinction or species invasion (Solé and Montoya 2001; Dunne et al. 2002, 2002b). In this example, the community S has a network S' and then realizes the property T of being "two-hubbed", which entails this fact about probability and then its stability.

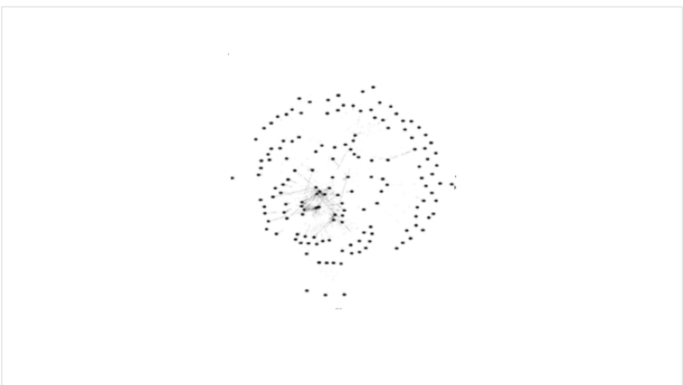

Figure 1 An ecological network in a community
(Silkwood Park, after Solé et al. 2002)

A network with such pattern is not a random network, like ones mostly considered by May (1977), who contested that diversity enforces stability. Most of the research about diversity and stability consisted therefore in exploring cases where networks of links depart from May's assumption that connections are random. A community whose associated network S' is an ecological scale-free network will have the property of stability against random extinction mentioned above. In this sense proving that a community is so structured triggers a topological explanation of its stability. This property is explanatory sufficient and one does not need to delve into the details of who is parasitic on whom, who preys on whom, etc., to establish the causes of stability. The details of these processes here do not make a difference, and the stability is not what eventually results from a sequence of causal interactions involving the species. Interesting parallels have been drawn between those networks and the Internet, as well as cell metabolic pathways and networks of words in texts (Solé and Valverde et al. 2001), or between ecological networks and financial networks (Levin et al. 2008),

especially regarding the stability requirements: all those systems realize the same topological properties, thus their stability is identically explained.

Considering small worlds, Montoya and Solé (2002) have shown that their structure happens in some communities and also yields forms of stability, because if you break some links between species, the structures allows for alternative links and therefore preserve the general stability. For example, suppose that a trophic web is a small world: between two given species you always have few nodes; if you delete one (e.g., you suppress the predator of A preyed on by B), in the cluster near the two unrelated nodes are many connections to be found so you can still find an alternative pathway. Hence, the property of the interaction network S' proper to a community S, of being a small world, explains why it is resistant to species deletion and invasion, thus why it is stable.

Suppose indeed that many different communities S_i of different species x_k have the same interaction network S', where a link is defined both by its relata and its strength. This network is a specific graph in an abstract space, and specific properties regarding weak links and high degree of clustering will entail the stability of the community. No matter which species x_k in a given S_i are connected through which links in the real web of relations realizing S', what matters for the outcome is only the general shape S' of the web of links, and the extent to which it has high degree of clustering and weak links, and this holds for those different communities S_j. To this extent, explaining by considering the topology of food webs, or more generally ecological links, abstracts away from the nature of causal relations, in the sense of the genuine ecological relations between definite species and the causal mechanisms at work within the community. Suppose that in S_1 half of the links are of predation, and in S_2 half of those links are of parasitism, and that the species implied in S_1 and S_2 are differing by 30%. If the interaction network S' is quite the same (more precisely, S'_1 and S'_2 belong to a same equivalence class regarding a property of having weak links and high degree of clustering), then stability in S_1 and S_2 is explained; a detailed understanding of the processes B_1 in or B_2, which are different in S_1 and S_2, will not add anything to the understanding of why S_1 or S_2 are stable. In this sense, mechanistic explanations are superfluous relative to this explanandum.

Explaining biological robustness

The stability of ecosystems provided us with a family of examples of powerful topological explanations. The explanandum, here, ranges under the rubric "stability" in the sense of "disposition to stay the same across changes, under some important ecological aspects", and the nature of those aspects define the various stability properties (e.g. resilience, constancy of biomass, etc.) that communities may possess. Given this characterization, ecological stability is however not the only kind of biological stability; the robustness of biological systems in general means something very similar. Recently we witnessed an inflation of research programs dealing with various kinds of *robustness* of systems *at all levels* of the biological hierarchy.

By "robustness" here, and in order to encompass many different researches in the field, I mean keeping some parameters stable in the face of changing values of variables, which precisely can mean two things: a "level" definition, in the sense that change in low level variables doesn't involve change in high level variables – for instance changing the identity of several species does not affect some general properties like biomass or abundance pattern; and a "functional" definition (Wagner, 2005): robust are those systems that are able to maintain (some of) their functions in the face of perturbations. Plausibly, the latter definition works better with physiological systems.

Canalization and homeostasis are time-honored well-known cases of robustness in living systems; however, properties of robustness have been found at many lower levels: within the metabolic networks of cells, at the level of the genome and its expression, and at the level of the genetic code and proteins. Very generally defined robustness properties range from nucleotides to ecosystems (Fig. 2), and they may require analogous or identical explanations in several cases. Wagner (2005) provides a groundbreaking synthesis of those findings. I here after give two examples of robustness at low level, and in the next paragraph provide a more systematic view of robustness research according to the explanatory distinction sketched above.

In general, researchers ask two types of questions about robustness at all levels: a. *proximate*: how is it ensured? and b. *evolutionary* – which breaks down into (b1), why has it evolved? And (b2) what role may it play in evolution?

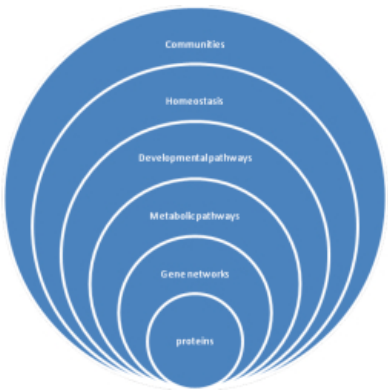

Fig. 2. Successive circles of robustness.

I will mostly consider here (a) and (b2). About (a), I claim that one can partition robustness into several classes, according to the explications for robustness, and whether they are topological or mechanistic (Table 1). And it may turn out that those classes are not concerned in the same manner by the two evolutionary questions (b). To show why those two kinds of explanations are held, let's consider two examples, which concern explaining the robustness of genetic sequences against mutations. If one identifies a feedback process that is triggered by the alteration of some nucleotide and leads to a restoration of some other genomic circuit, which then leads to the initial phenotypic state, this would clearly be a mechanistic explanation. On the other hand, an explanation, instead of appealing to any mechanism, may simply cite some properties of the genetic code, namely, the redundancy of some triplets of nucleotides coding for amino acids. What is at stake here are the properties of the mapping between DNA sequences and proteins: due to redundancy, which is a topological property of this mapping, many random changes in nucleotides will not change anything because they will turn a codon into a synonymous codon. This explanation works in the same way as the quasi-scale-free network explanation of stability of some ecosystems, and does not need the unraveling of any specific causal interaction.

At many levels of the biological hierarchies, you can find these two kinds of explanations of robustness coexisting, as is shown in Table 1. This is exactly like

regarding the explanation of community stability, one can either identify a feedback mechanism, starting from the extinction of a species, and leading to the replacement by a functionally equivalent species, via the creation of a vacant niche and the increased probability for a speciation towards a new species filling this niche (mechanistic explanation), or turn to the topological properties of the ecological web as explanatory (topological explanation).

Mechanisms	**Topology**
• Feedback control (physiological homeostasis; lactose operon)	• Modularity
• DNA repair systems (-> fct of sex (Michod and Bernstein 1996))	• Redundancy
	• Small world topologies

Table 1.Kinds of explanations of biological robustness.

The philosophical main point here, is that topological explanations are overrepresented when it comes to explain robustness, because they are very well fit to explain robustness, since robustness is a kind of invariance, and topological properties are in general specifying invariances (therefore allowing to define equivalence classes, be it in classical topology or in graph-theory).

Conclusions

This paper intended to make sense of a difference between two kinds of explanation: mechanistic ones, absolutely pervasive in natural sciences and aiming to display causal processes responsible for an explanandum – and topological ones, which do not consider mechanisms at stake. The latter kind is more and more frequent because of both the science of networks, which emerged in the wake of the general focus on complexity – and the "neutrality" theme in ecology and biology. An important part of the explanations of robustness of many kinds (resilience, stability, etc.) in many systems relies on topological considerations.

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